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Non-native spiders change assemblages of Hawaiian forest fragment kipuka over space and time

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Abstract

We assessed how assemblages of spiders were structured in small Hawaiian tropical forest fragments (Hawaiian, *kipuka*) within a matrix of previous lava flows, over both space (sampling kipuka of different sizes) and time (comparison with a similar study from 1998). Standardized hand-collection by night was carried out in May 2016. In total, 702 spiders were collected, representing 6 families and 25 (morpho-)species. We found that the number of individuals, but not species richness, was highly correlated with the area of sampled forest fragments, suggesting that kipuka act as separate habitat islands for these predatory arthropods. Species richness was significantly lower in the lava matrix outside the kipuka compared to the kipuka habitats, although there was no statistical difference in species composition between the two habitats, largely because of similarity of non-native species in both habitats. Over the last 20 years, the abundance of non-native spider species substantially increased in both kipuka and lava habitats, in marked contrast to the vegetation that has remained more intact. With endemicity of terrestrial arthropods reaching over 95% in native forests, non-native predatory species present a critical challenge to the endemic fauna.

Keywords

Araneae, diachronic study, island

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Introduction

Kipuka are small tropical forest fragments surrounded by recent lava flows on Hawaiian islands. Many of these kipuka are rich ecosystems that have been previously investigated for their importance for native passerine birds, plants (trees and ferns) and picture-winged flies (e.g. Muir and Price 2008). Due to their spatial arrangement in a volcanic matrix, kipuka can be considered as islands within islands (Tielens et al. 2019), and thus consequently important, and original, to test classical assumptions regarding the combined effects of area and isolation on species assemblages.

The kipuka system might also be used to examine whether such particular habitats retain a strong biotic resistance to non-native species. In Hawaii, due to the remote localization of this archipelago, there are well known impacts of non-native species, with most of these studies focusing on changes in ecosystem structure (e.g. Krushelnycky and Gillespie 2008). Indeed, multiple ecological impacts of non-native flora and fauna threaten communities world-wide, and can be potentially even damaging to island systems (Vitousek 1988). Although some non-native species are reported from kipuka (e.g., rats and other mammals), kipuka appear to be less vulnerable to non-native than other (lowland) habitats, with, for example, non-native plant species almost entirely absent from kipuka (Flaspohler et al. 2010). To the best of our knowledge, no study has yet assessed how non-native spiders colonized kipuka, although they represent a major group of predators in this habitat, potentially reducing native populations.

In this study, we examined how assemblages of spiders are structured over space (e.g., comparisons across kipuka as well as lava matrix), but also potentially changed over time (in comparison to a previous study during the 1990s in the same study site: Vandergast and Gillespie 2004). We tested the general hypothesis suggested by observations of relatively intact native biota (Krushelnycky and Gillespie 2008, Flaspohler et al. 2010), that kipuka function as islands with strong biotic resistance to arthropod non-native species. More precisely, our expectations are that 1) abundance and species richness increase with increasing kipuka area, 2) species composition and richness differ between kipuka habitat and the surrounding areas and 3) despite an overall increase in non-native spider species over the last decades, the increase is less in kipuka habitats than outside.

Materials and methods

Study site and collecting

Fieldwork was conducted on the youngest and largest island of the Hawaiian Archipelago, Hawaii or the Big Island. The Kipuka system investigated consists of forest fragments surrounded by an 1855–1856 lava flow originating from Mauna Loa Volcano (19°40'01"N, 155°20'56"W). These forest fragments grow on 3,000–5,000 years

BP soil (Vitousek 2004), range in age from approximately 750–1,500 year BP and were most likely connected before the 1855–1856 flow that currently surrounds them (Trusdell and Lockwood 2017). These kipuka occur within the State of Hawaii Forest Reserve System (Upper Waiakea Forest Reserve), along the Daniel K. Inouye Highway (formerly Saddle Road; mile marker 16–18, Kaumana Trail).

The forest fragments' plant species composition is relatively constant across forest fragments (Raich et al. 1997) and is categorized as mesic to wet *ohia* (*Metrosideros polymorpha,* Myrtaceae) forest (Jacobi and Warshauer 1990). Soil characteristics are also quite constant across fragments (Raich et al. 1997) but soil nutrient conditions may vary (Vannette et al. 2016). Surrounding these fragments, the lava matrix is a rough textured patchwork of undulating mounds of smooth lava and free chunks of very angular pieces, extremely porous where the vegetation is sparser and poorer than those of the fragments (for a detailed description of both habitats, see Vandergast and Gillespie 2004; Flaspohler et al. 2010; Vaughn et al. 2014).

Vegetation-dwelling assemblages of spiders were collected in May 2016 in the kipuka fragments and outside, in the surrounding lava, of five small (<1 ha) and five large forest patches (2–11 ha) along the Saddle Road (mile marker 16–18: Kaumana trail). The influence of kipuka area on both species richness and abundance of spiders was tested using linear regressions. Kipuka area was estimated using airborne LiDAR (Light Detection and Ranging) technology as reported by Flaspohler et al. (2010).

Field collection involved beating vegetation at night, the best time for collecting spiders. Each kipuka and surrounding lava was sampled by 2 people for a total of 30 min, a time determined following initial sampling. Individuals were collected separately in ethanol for identification to species or morpho-species (i.e., spider family) level at the lab. During identification, specimens were checked against voucher specimens obtained/used in the previous study (Vandergast and Gillespie 2004). All specimens are stored at the University of Rennes, France.

Data analysis

The influence of kipuka size on both species richness and abundance of spiders was tested using linear regressions. Paired T-tests and Permanova (1000 permutations) were used to test for differences in species richness and composition, respectively, between the two habitat types. Non-metric multi-dimensional scaling ordination was used to visualize spider assemblages in the two habitats. 'Indigeneity status' was assessed using multiple bibliographic sources (see details in Vandergast and Gillespie 2004), combined with the expertise of one of the authors (RG). The proportion of native vs non-native species was compared between kipuka and lava habitats in the same area in 2016 as had been compared in 1998 (from Vandergast and Gillespie 2004) using χ^2 tests. To allow a direct comparison of kipuka and lava habitats with previous sampling we pooled the two kipuka sampling categories of "core" and "edge" reported in the earlier study.

Results

In total, 702 spiders belonging to 6 families and 25 (morpho-) species were collected (see details in Table 1).

Kipuka size had a large effect on the number of individuals (linear regression, Y = 5.58X(ha) +27.4 , R^2 = 0.93, p < 0.001, 9 df), but no effect on species richness (linear regression, R^2 = 0.12, NS, 9 df). Species richness of spiders was significantly higher in kipuka habitats compared to the surrounding lava (Mean±SE: 10.8 ± 0.6 *vs.* 6.8 ± 0.6 respectively; Paired T-test, t = 6.34, 9 df, p < 0.001), although there was no statistical difference in species composition between the two habitat types (Permanova: F1,8 = 0.06, p = 0.349, Fig. 1). The proportion of non-native spider species increased significantly between 1998 and 2016, in both kipuka and lava habitats (χ^2 tests, χ^2 = 67.53, 1 df, p < 0.001 and χ^2 = 4.34, 1 df, p < 0.037 respectively), with a higher increase in kipuka habitats (see Fig. 2). This increase in both habitat types was due to both an increase in the number of non-native species and a particular increase in the number of individuals of few species (e.g. *Steatoda grossa*: Table 1).

Table 1. Number of individuals, status (Na = Native, Nn = Non-native, *: species not found in 1998, according to Vandergast and Gillespie 2004) and code of spider taxa collected inside and outside the kipuka.

Family	Genus	Species	Status	Nind (kipuka)	Nind (lava)	Code
Araneidae	*Cyclosa*	sp.	Na	21	51	Cycsp
	Neoscona	sp1	Nn	42	1	Neosp1
		sp2	Nn*	23	31	Neosp2
Linyphiidae	*Agyneta*	sp.	Nn*	3	0	Agysp
Miturgidae	*Cheiracanthium*	sp.	Nn*	1	13	Chesp
Philodromidae	*Pagiopaplus*	sp.	Na*	4	0	Pagsp
Tetragnathidae	*Tetragnatha*	*acuta*	Na	56	85	Tetac
		anuenue	Na	43	44	Tetan
		brevignatha	Na	26	0	Tetbr
		hawaiiensis	Na	21	0	Tetha
		quasimodo	Na	27	6	Tetqu
		spp.	Na	2	0	Tetsp
Theridiidae	*Argyrodes*	sp.	Na	1	0	Thesp7
	Ariamnes	spp.	Na*	59	1	Argspp
	Steatoda	*grossa*	Nn*	11	0	Stegr
	Theridion	*grallator*	Na	20	0	Thegr
		sp1	Na	23	35	Thesp1
		sp2	Na	8	2	Thesp2
		sp3	Na	1	0	Thesp3
		sp4	Na	4	2	Thesp4
		sp5	Na	4	6	Thesp5
		sp6	Na	2	3	Thesp6
Thomisidae	*Mecaphesa*	sp1	Na*	1	3	Mecsp1
		sp2	Na*	4	10	Mecsp2
	Synaema	sp.	Na*	1	1	Synsp

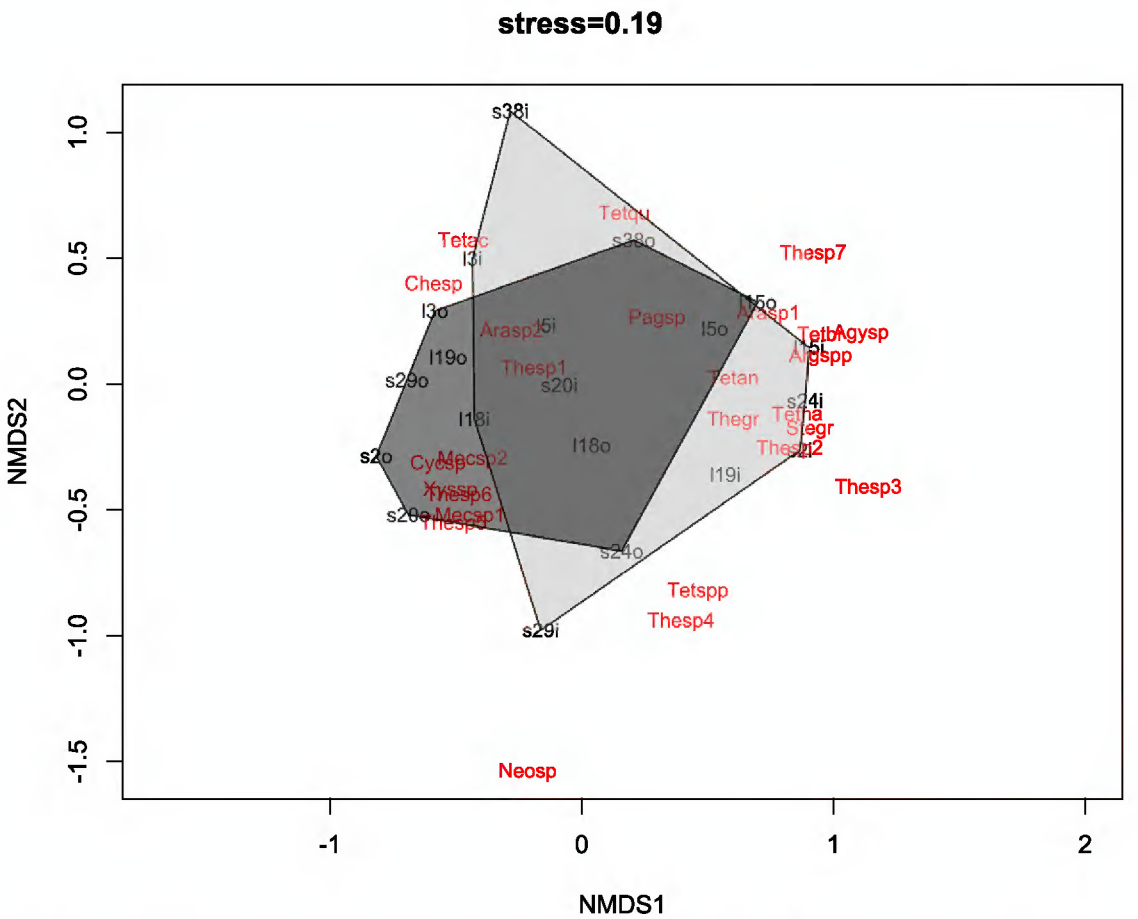

Figure 1. Non-metric multi-dimensional scaling ordination of spider assemblages from kipuka habitats (grey ellipsoid) and surrounding lava (black ellipsoid). Species are in red and sampling stations in black. Stress = 0.189. For spider taxa code, see Table 1.

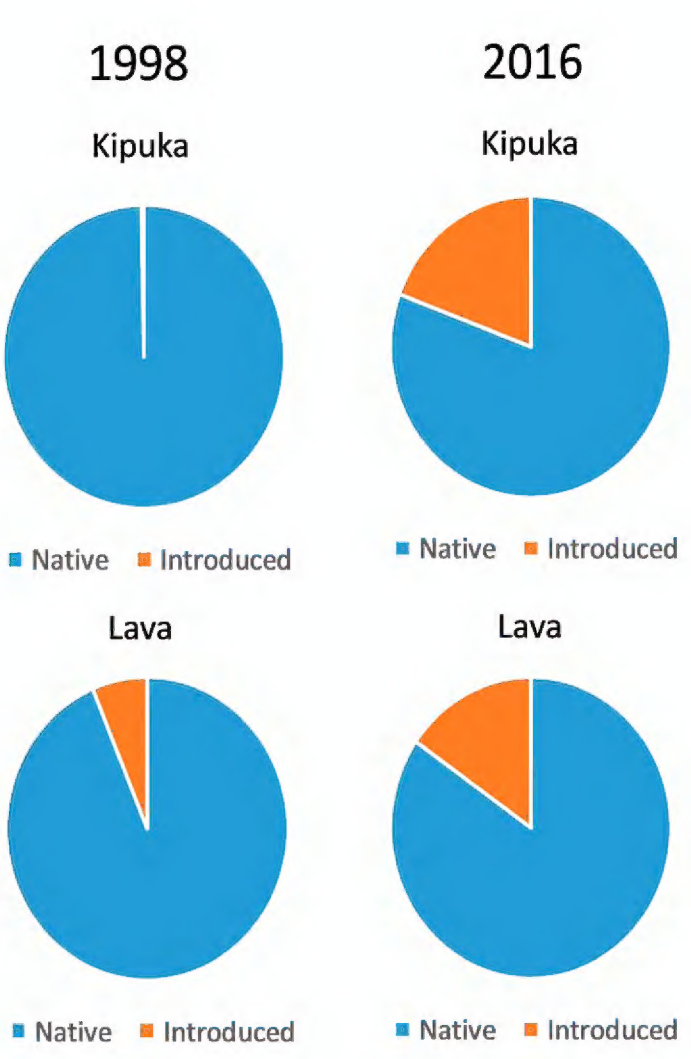

Figure 2. Relative abundance of native (blue) and non-native (orange) species in kipuka habitats and surrounding lava, in 1998 (430 individuals) and in 2016 (702 individuals).

Discussion

The total number of individuals across all spider species was strongly associated with the area of sampled forests, suggesting that kipuka act, at least partly, as separate habitat islands for the spiders. Yet, as recently observed for entire arthropod communities in the same area (Tielens et al. 2019), spider species richness was not a function of kipuka size. Indeed, spider species in kipuka habitats tend to be found in all such habitats (Vandergast and Gillespie 2004, Vandergast et al. 2004). These two results altogether suggest that kipuka act as islands for native species in a hostile matrix. Yet, the abundance of several native and non-native species was found to be high in both kipuka habitats and surrounding lava, leading to overlapping, and statistically indistinguishable, assemblage compositions (see also Tielens et al. 2019). Fragment size is known to be a strong determinant of the structure of the forest in the kipuka (Vaughn et al. 2014) with larger fragments having greater average height, larger diversity of height and lower edge to core habitat being thus less affected by the matrix overall. Kipuka edges are also known to house different species from the kipuka interiors (Vandergast and Gillespie 2004). For example, more native *Drosophila* are found in large kipuka while more non-native *Drosophila* and other insects are found in small kipuka (Mueller 2015). Patch size, on top of influencing habitat quality, is also known to act on migration rates, and the linear relationships between kipuka area and number of spider individuals can also be the result of immigration-emigration dynamics (Hambäck and Englund 2005).

There was an important increase in the proportion of non-native species over time, while no native species disappeared between the two sampling periods. Several new species like *Cheiracanthium* sp. and *Steatoda grossa* were detected in this study, i.e. they were not recorded in the same study site twenty years ago. Other species have an unclear biogeographic and taxonomic status, e.g. *Agyneta* sp., which shows that more intensive studies are still needed on the Hawaiian archipelago (Gertsch 1973). The kipuka we sampled belong to the State of Hawaii Forest Reserve System (Upper Waiakea forest reserve), an area subject to limited anthropogenic disturbance for the last 160 years, but strategically located along the Daniel K. Inouye Highway that was reconstructed in 2008 and 2011. Thus, the increase of non-native species is likely associated with previous construction activity and more road traffic along the renovated highway. Non-native arthropods in Hawaii respond more quickly to disturbance than their endemic counterparts (Gillespie et al. 2008) and are known to follow pathways of human activity (Krushelnycky and Gillespie 2008). Interestingly, the increase in non-native spiders was actually higher in kipuka habitats compared to the outside lava, rejecting our hypothesis of a stronger biotic resistance to non-native species in intact forest fragments, and in marked contrast to the relatively intact flora of these habitats. Kipuka offer many micro-habitats for newcomers, for example, bark of *Metrosideros polymorpha* where *Steatoda grossa* are often found in numbers, as well as complex edge habitats where one species of non-native spiders was found previously (Vandergast and Gillespie 2004).

In conclusion, kipuka function as habitat islands within islands, with many island-like features such as a characteristic biota, unique microclimate, and biological associations with increasing area. Kipuka, like other island-shaped habitats, also appear to be vulnerable to non-native species, especially as compared to the surrounding lava. Until now native species of spiders do not seem to have been affected by these newcomers, but spiders can have a large impact on prey species because they are ecologically dominant and generalist predators in a large variety of habitats (Pekár and Toft 2015), including tropical forests (Coddington et al. 2009). In Hawaii, with a large number of endemic species (Howarth 1990, Eldredge and Evenhuis 2003), non-native spiders are a critical challenge for management. The impact of these new generalist predators on the structure and functioning of kipuka is currently investigated using meta-barcoding and NGS techniques. We are also planning to look at other spider associates, including parasite occurrence in spiders (see Vandergast and Roderick 2003), to see how the associated community has changed together with increased non-native species.

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